

ELECTRONIC SUPPLEMENTARY MATERIAL 2

Evolution of dinosaur epidermal structures

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1. DINOSAUR PHYLOGENY

In the absence of a current comprehensive dinosaur supertree, we constructed an informal consensus tree of dinosaur relationships in order to examine the evolution of integumentary structures in the clade. A broad-scale ornithischian phylogeny [1] forms the overall framework for the latter clade with additional information on in-group relationships among hadrosaurs [2,3], ceratopsians [4], stegosaurs [5], ankylosaurs [6] and *Kulindadromeus* [7] from other recent sources. Sauropodomorph interrelationships are based on ref. 8. Theropod relationships are based on two primary sources: one dealing largely with major divergences in Tetanurae [9] and the other with coelurosaurian interrelationships [10].

2. ADDITIONAL COMMENTS ON TAXA INCLUDED

Many dinosaur tracks show evidence of skin impressions, but these were disregarded and excluded from the analysis, as they are squamous in all taxa. Moreover, attributing dinosaur tracks to species based on body fossils is highly problematic. Unfortunately, the only records of Late Triassic skin impressions are currently from dinosaur tracks.

In some cases, organic trace fossils are preserved in association with skeletal remains that show the presence of a skin envelope around a body fossil, but the morphologies of the skin structures (i.e. feathers vs scales) were not preserved. These inconclusive traces were also excluded from the analyses.

Several small-bodied ornithischian taxa with soft-tissue preservation (*Kulindadromeus*, *Kulindapteryx* and *Daurosaurus*) have been named from the Ukureyskaya Formation of Russia [7,11], and each has been assigned a different phylogenetic position: *Kulindadromeus* as a basal cerapodan [7], *Kulindapteryx* as a jeholosaurid ornithopod [11] and *Daurosaurus* as a hypsilophodontid ornithopod [11], although the affinities of the latter two taxa were not assessed in the context of a phylogenetic analysis. However, given the similarities between the described material (not least in their integumentary structures) and the fact this deposit probably represents a monodominant bonebed [7], it seems most likely that these taxa are synonymous, although this suggestion requires further detailed investigation. As taxonomic revision of this material lies outside the remit of this paper, we include all three species in our database separately, but include only *Kulindadromeus* in our analyses, as it is the only one of these taxa to be have been included in a

phylogenetic analysis.

Although the integumentary features of *Xiaotingia* are poorly preserved and their detailed structure cannot be determined, they demonstrate that some kind of filamentous or branched structures were present in this taxon [12]. Rather than assume the presence of more derived branched structures, we scored these features as filamentous in our analyses, as a proxy for the character state ‘feathers present, but structure unknown’. Scoring this taxon with the ‘branched feather’ state would increase the already very high support values for the presence of this feature in this part of the dinosaur tree.

3. DEPOSITIONAL ENVIRONMENT

The physical and chemical conditions of the depositional environment are likely to exert an influence on integument preservation. In order to test this assumption, we collected generalized information on the depositional environments yielding each of the dinosaur taxa listed in our database. Environments were divided into two broad categories: lagoonal/lacustrine (representing low-energy environments with fine-grained sediments) or alluvial (representing high-energy environments with coarse-grained sediments, such as channel sandstones or overbank mudstones). All taxa could be scored for this information, so there are no missing data (Table S1). A chi-squared analysis was performed to test the null hypothesis that there was no difference in the frequency of scale or feather preservation in taxa occurring in lagoonal/lacustrine or alluvial environments.

Table S1. Contingency table for chi-squared analysis testing relationship between depositional environment type and numbers of taxa exhibiting preservation of feathers/filaments/quills or scales. Information taken from Electronic Supplementary Material (ESM) 1. Note that *Psittacosaurus* occurs in the table twice, as it has both scales and ‘quills’.

	Taxa with filaments	Taxa with scales	Total
Alluvial	2	47	49
Lacustrine/lagoonal	29	3	32
Totals	31	50	81

This analysis rejected the null hypothesis ($p < 0.0001$), suggesting that depositional environment and integumentary preservation are correlated and need to be taken into account when discussing the presence/absence of dinosaur integumentary structures (see main text for discussion).

4. BODY REGION AND INTEGUMENT

It is possible that different integument types were associated with particular body regions in dinosaurs. Consequently, if one of these key regions was not preserved in a particular taxon this might introduce a systematic bias into our analysis by introducing false absences for integumentary features. In order to identify any such bias, we recorded the distributions of integumentary structures by body region as preserved in each taxon (see ESM 1). Body regions selected were: forelimb, hind limb, axial dorsal (skull, neck and dorsum), axial ventral (underside), and tail. Note that the same taxa may be counted multiple times if they preserve skin in multiple regions. As many taxa lack all body regions, approximately 65% of the body regions

listed for all taxa included could not be scored (around 60% if the ‘Unrecorded’ body region is removed). We used a chi-squared analysis to test the null hypothesis that all integument types would be similarly distributed among all body regions (Table S2).

Table S2. Contingency table for chi-squared analysis testing relationship between preserved body region and recorded integument type. Note that in some cases skin preservation is mentioned for a particular taxon, but the authors do not record the type of structures preserved (it may be an organic, structureless film, for example) or where it occurs on the body. These occurrences are listed in the ‘Indeterminate’ and ‘Unrecorded’ data cells. Information taken from ESM 1.

	Indeterminate	Scales	Filaments	Feathers	Totals
Axial dorsal	4	27	16	4	51
Axial ventral	1	16	9	3	29
Forelimb	1	11	7	10	29
Hind limb	0	14	6	7	27
Tail	0	14	8	10	32
Unrecorded	3	9	1	0	13
Totals	9	91	47	34	181

Results from the chi-squared analysis of this data indicate that the null hypothesis can be rejected, as a significant correlation between preserved body region and the type of integument it possesses was recovered ($X^2 = 31.6$, $p = 0.007236$). However, further scrutiny suggested that the inclusion of data from the ‘unrecorded’ body region and indeterminate skin types were largely responsible for this result. As this data is of questionable value (given its ambiguous nature), we excluded it and re-ran the analysis using the modified dataset in Table S3.

Table S3. Contingency table for chi-squared analysis testing relationship between preserved body region and recorded integument type, excluding data on indeterminate skin impressions and those occurring in an unrecorded body region. Information taken from ESM 1.

	Scales	Filaments	Feathers	Totals
Axial dorsal	27	16	4	47
Axial ventral	16	9	3	28
Forelimb	11	7	10	28
Hind limb	14	6	7	27
Tail	14	8	10	32
Totals	82	46	34	162

Reanalysis of this reduced dataset reveals that the correlation is no longer significant ($X^2 = 12.7$, $p = 0.1239$) and that the null hypothesis cannot be rejected. If filaments and feathers are combined into a single category (representing a set of taxa with complex integumentary structures) the results become even less significant ($X^2 = 3.4$, $p = 0.4913$). As there appears to be no body region that preferentially preserves scales, filaments or feathers, we can reject the hypothesis that preferential preservation of particular body regions might affect the outcome of our analyses.

5. MAXIMUM-LIKELIHOOD AND PARSIMONY ANALYSES

The full maximum likelihood results from these analyses are presented in numerical form in ESM 1 and in diagrammatic form in figures S1–S18. As a secondary assessment of ancestral distributions, character evolution was also interpreted using traditional parsimony approaches (Fitch, ACCTRAN and DELTRAN [13]). All parsimony-based analyses recovered scales as the primitive condition for Dinosauria or found the condition at this node to be ambiguous, and filaments and feathers optimized as a synapomorphy of either Tetanurae or Coelurosauria (see Table S4). These results are congruent with those obtained from the maximum-likelihood analyses. Ambiguities in resolution result where pterosaurs are assumed to be primitively filament-covered, unscored the importance of this feature in understanding skin evolution in dinosaurs. Nevertheless, many optimisations involving filament-covered pterosaurs still recover dinosaurs as primitively scaled.

Multistate : Scales : unordered : MBL

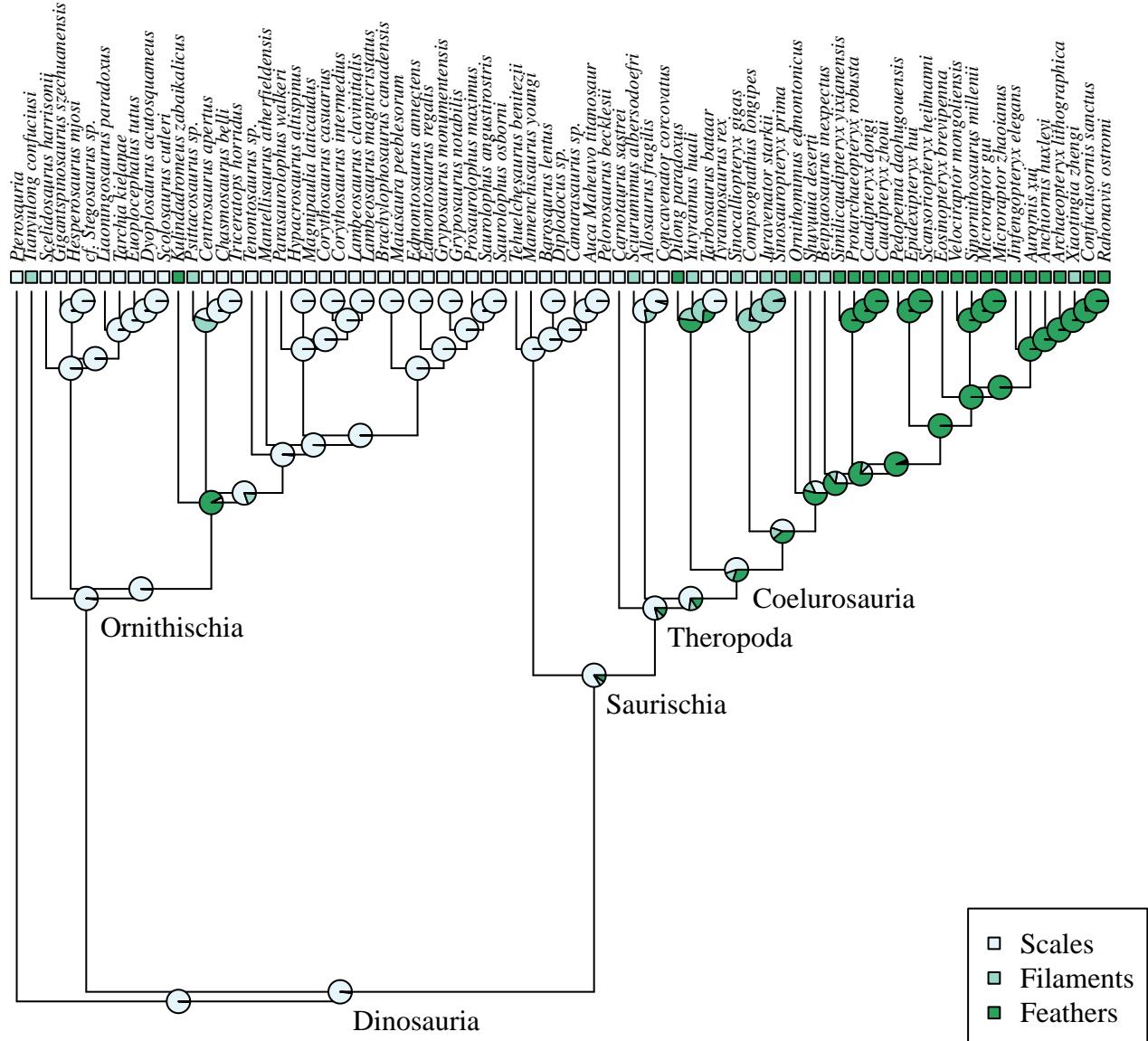


Figure S1. Ancestral states reconstructions using maximum likelihood along a time-scaled tree using the 'mbl' time-scaling method. Integument is treated as an unordered multistate character and the outgroup (Pterosauria) is coded as primitively scaled.

Multistate : Scales : ordered : MBL

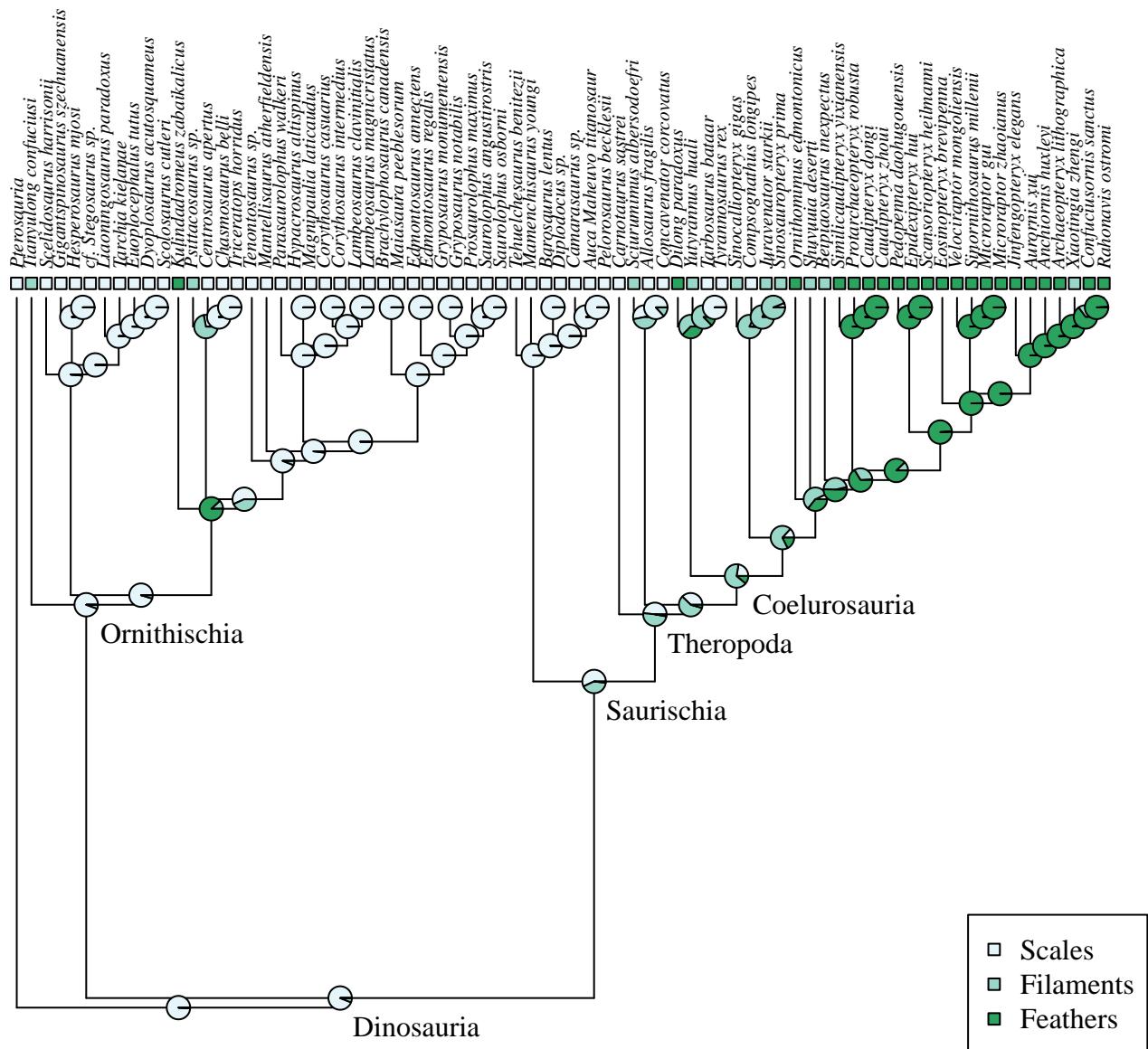


Figure S2. Ancestral states reconstructions using maximum likelihood along a time-scaled tree using the 'mbl' time-scaling method. Integument is treated as an ordered multistate character and the outgroup (Pterosauria) is coded as primitively scaled.

Binary : Scales : unordered : MBL

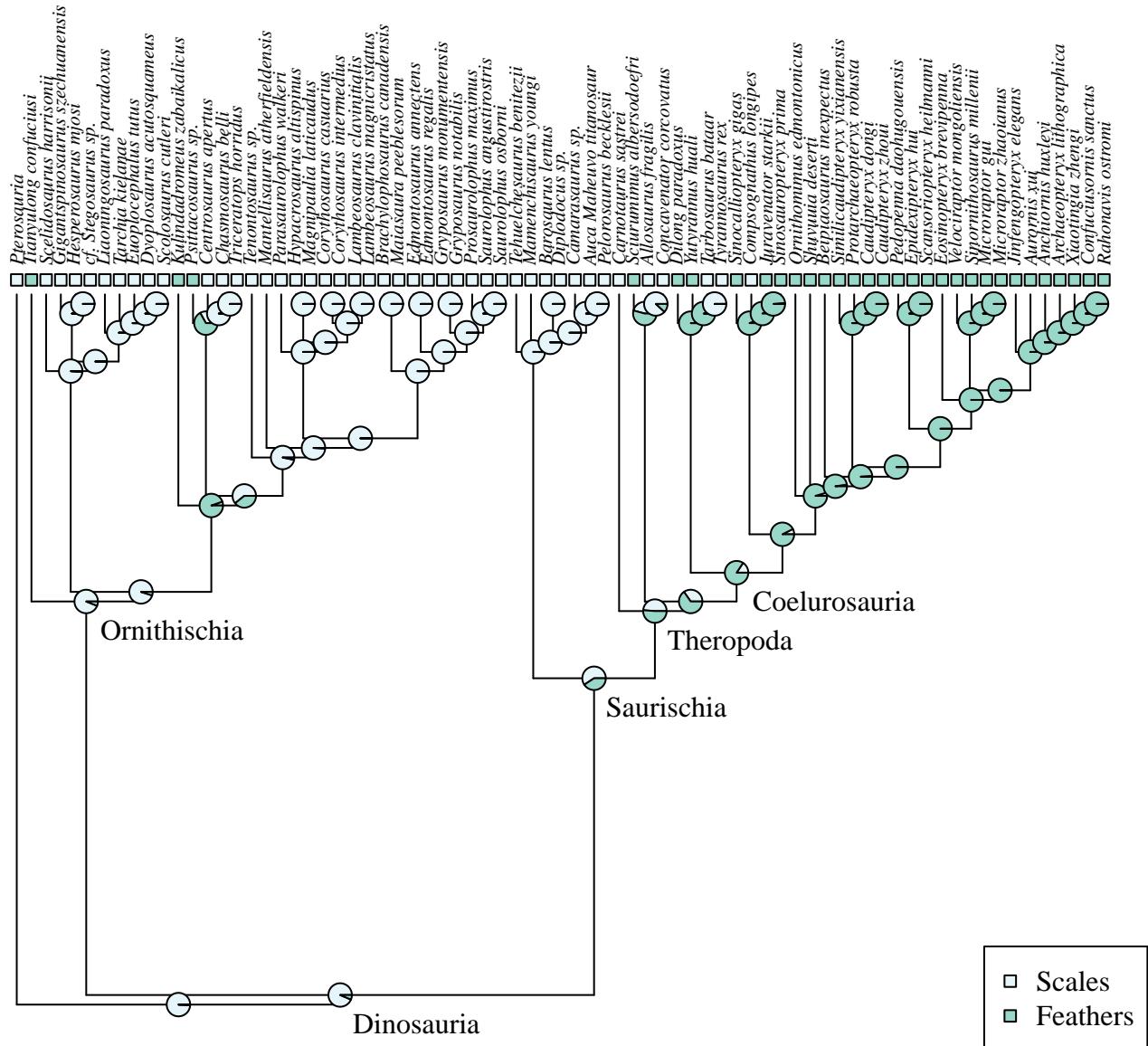


Figure S3. Ancestral states reconstructions using maximum likelihood along a time-scaled tree using the 'mbl' time-scaling method. Integument treated as a binary character and the outgroup (Pterosaura) is coded as primitively scaled.

Multistate : Filaments : unordered : MBL

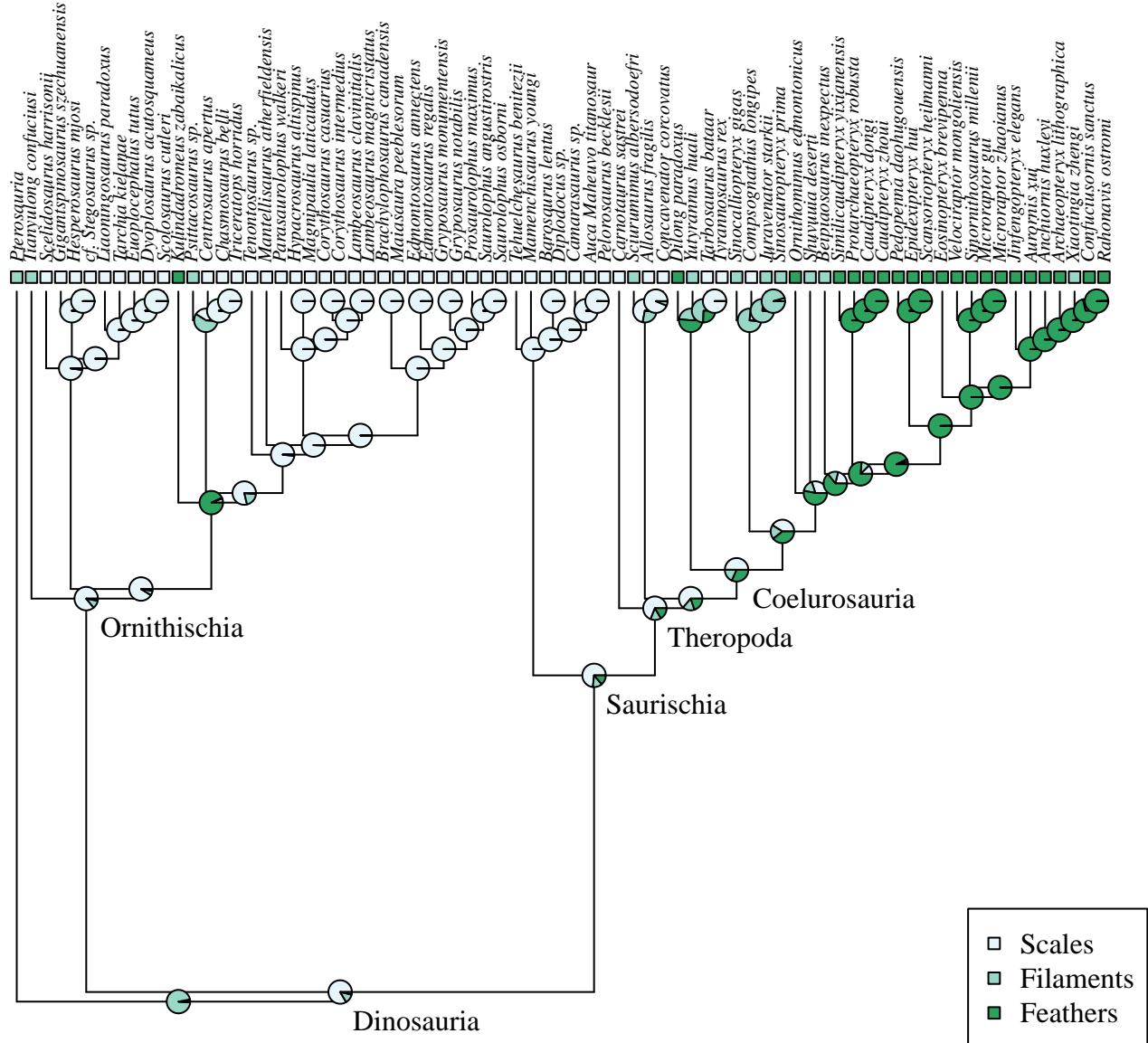


Figure S4. Ancestral states reconstructions using maximum likelihood along a time-scaled tree using the 'mbl' time-scaling method. Integument treated as an unordered multistate character and the outgroup (Pterosauria) is coded as primitively filamented.

Multistate : Filaments : ordered : MBL

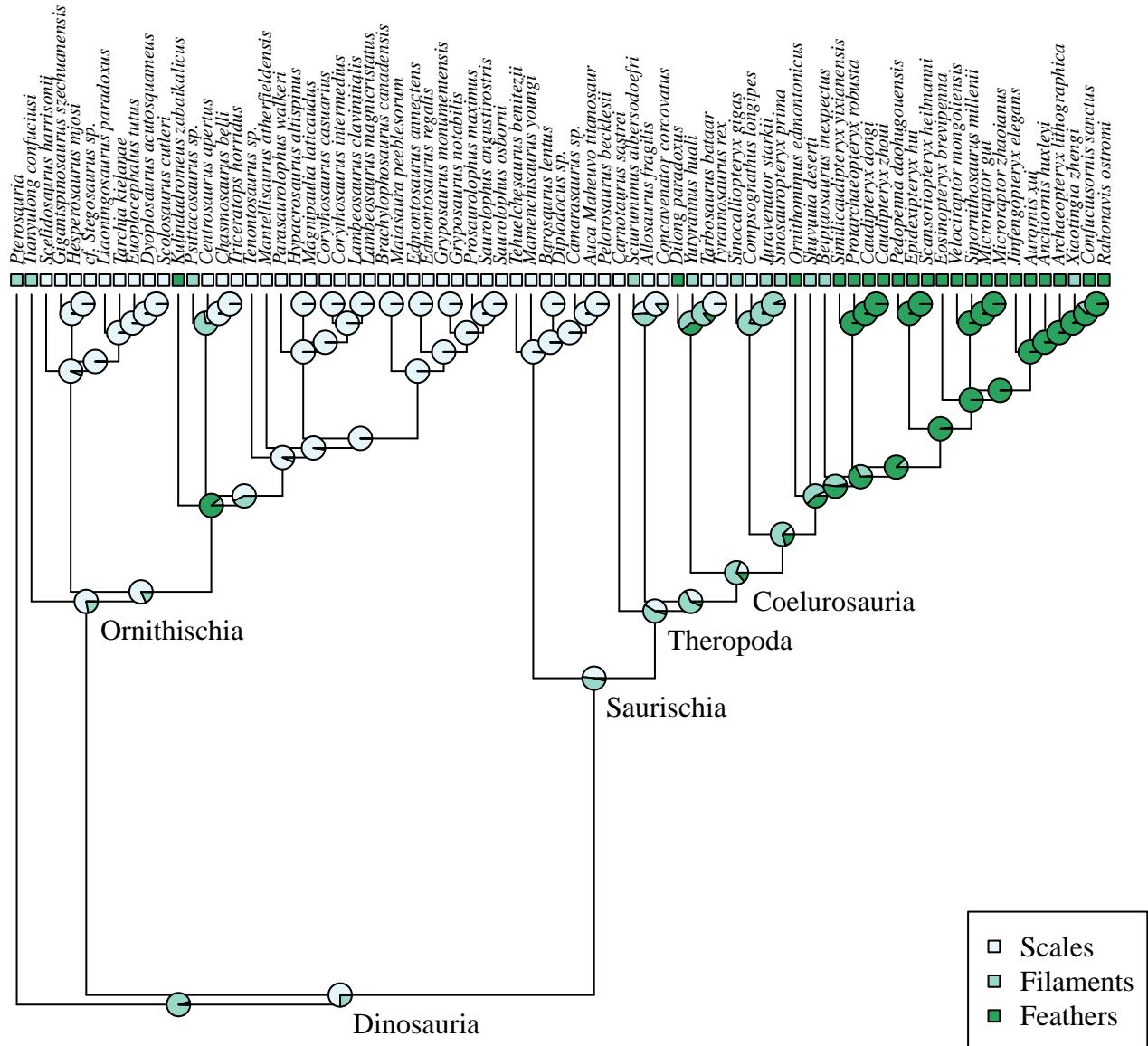


Figure S5. Ancestral states reconstructions using maximum likelihood along a time-scaled tree using the 'mbl' time-scaling method. Integument treated as an ordered multistate character and the outgroup (Pterosauria) is coded as primitively filamented.

Binary : Filaments : unordered : MBL

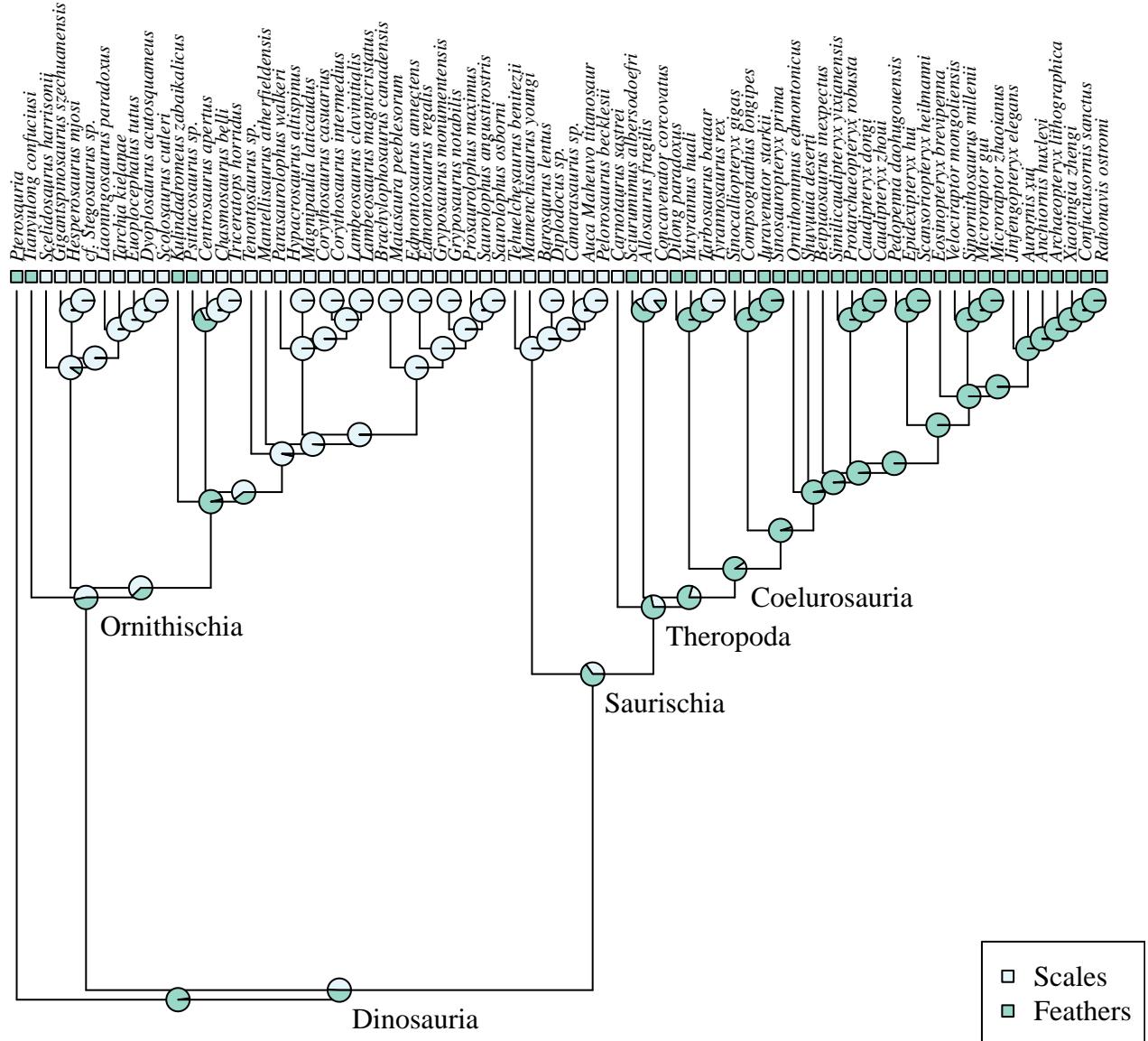


Figure S6. Ancestral states reconstructions using maximum likelihood along a time-scaled tree using the 'mbl' time-scaling method. Integument treated as a binary character and the outgroup (Pterosauria) is coded as primitively feathered.

Multistate : Scales : unordered : Equal

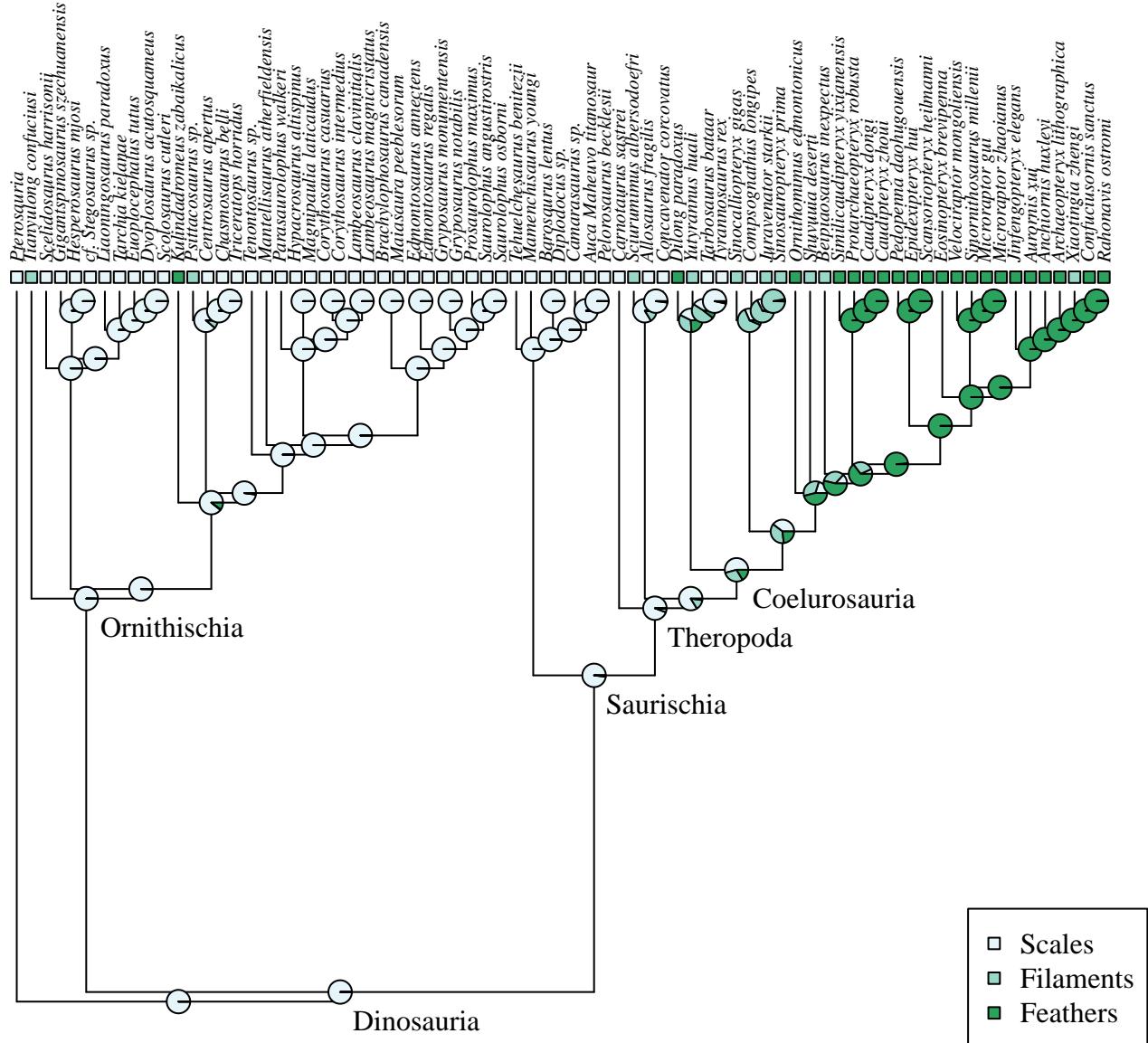


Figure S7. Ancestral states reconstructions using maximum likelihood along a time-scaled tree using the 'equal' time-scaling method. Integument treated as an unordered multistate character and the outgroup (Pterosauria) is coded as primitively scaled.

Multistate : Scales : ordered : Equal

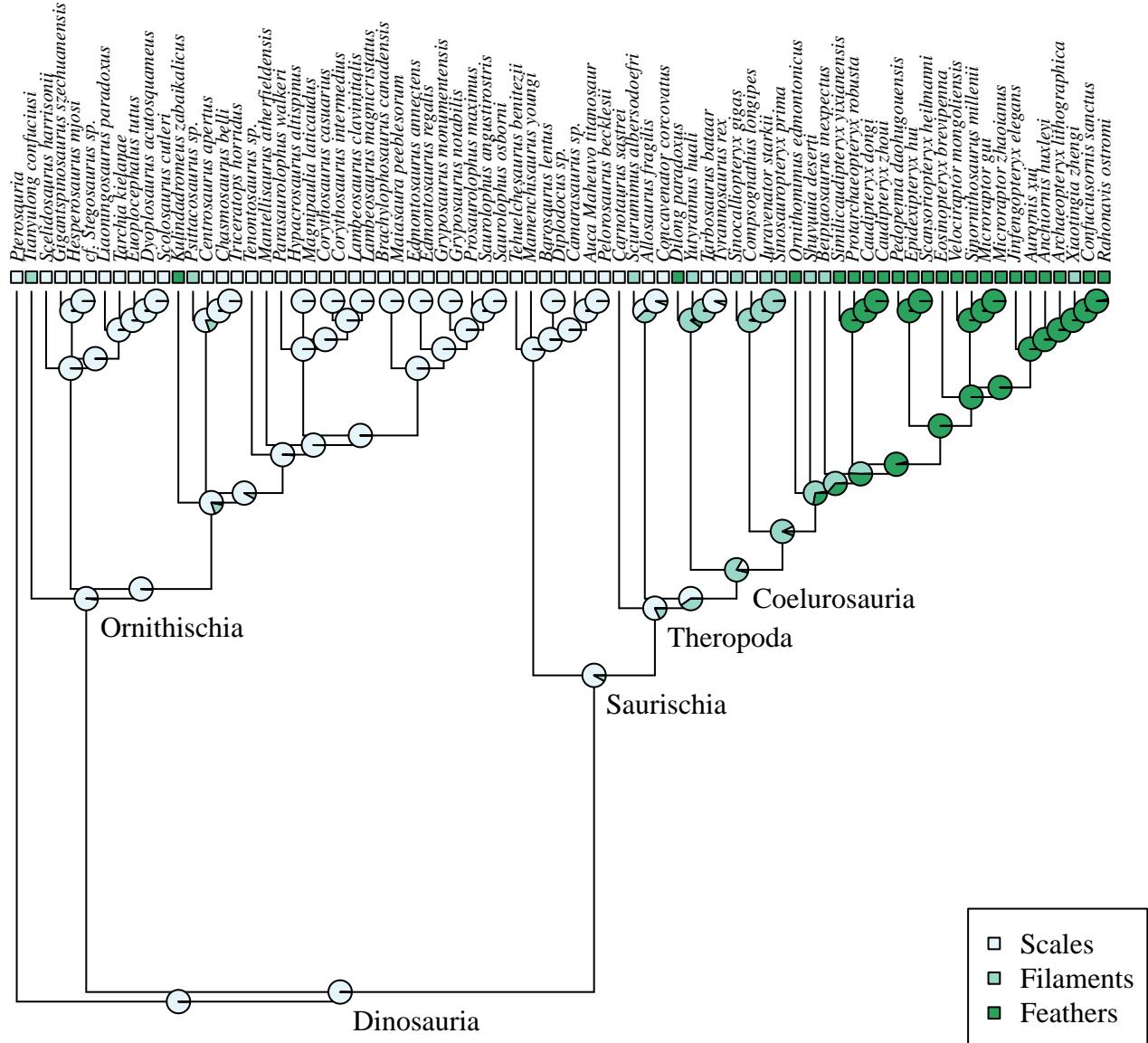


Figure S8. Ancestral states reconstructions using maximum likelihood along a time-scaled tree using the 'equal' time-scaling method. Integument treated as an ordered multistate character and the outgroup (Pterosauria) is coded as primitively scaled.

Binary : Scales : unordered : Equal

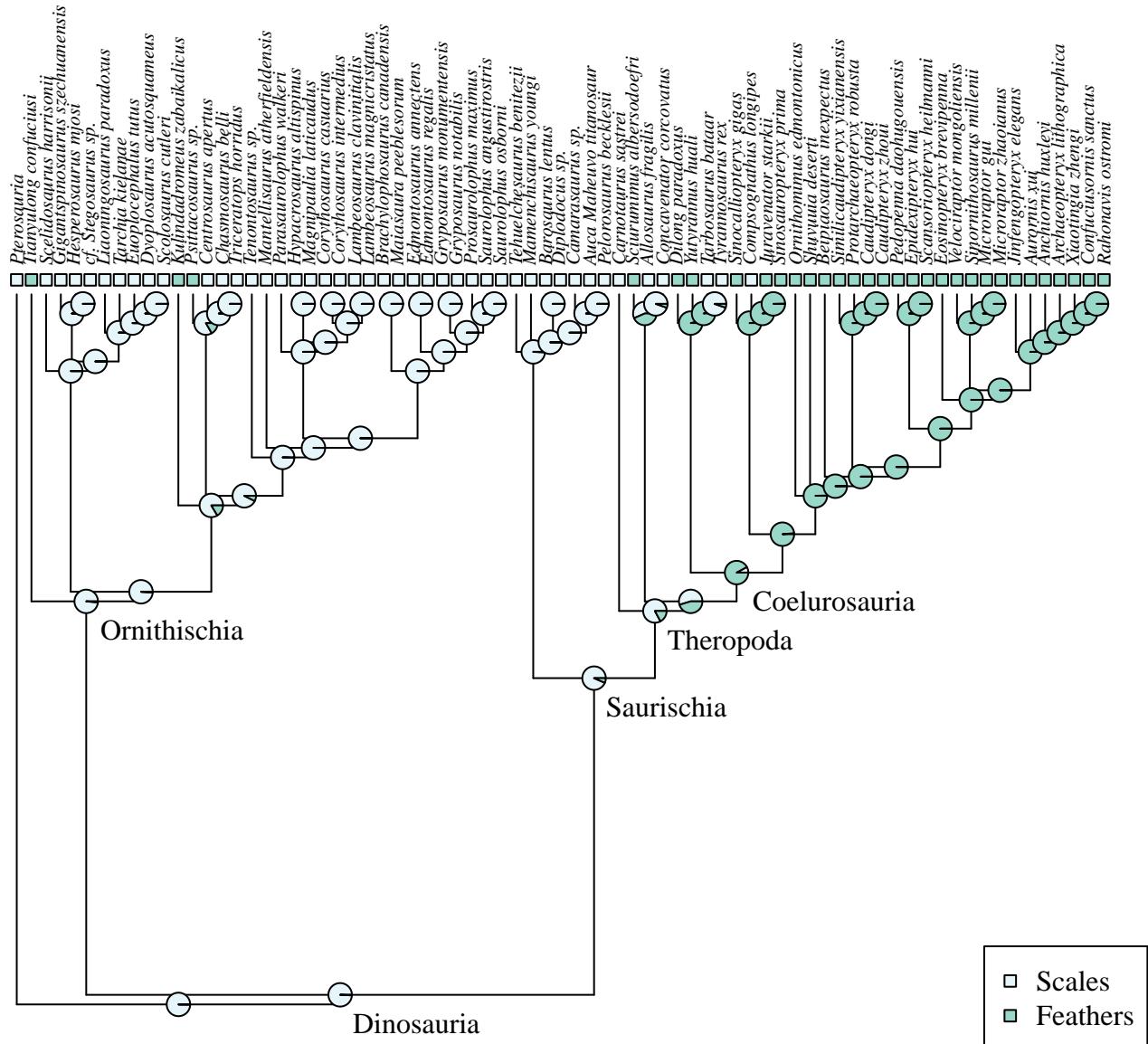


Figure S9. Ancestral states reconstructions using maximum likelihood along a time-scaled tree using the 'equal' time-scaling method. Integument treated as a binary character and the outgroup (Pterosaura) is coded as primitively scaled.

Multistate : Filaments : unordered : Equal

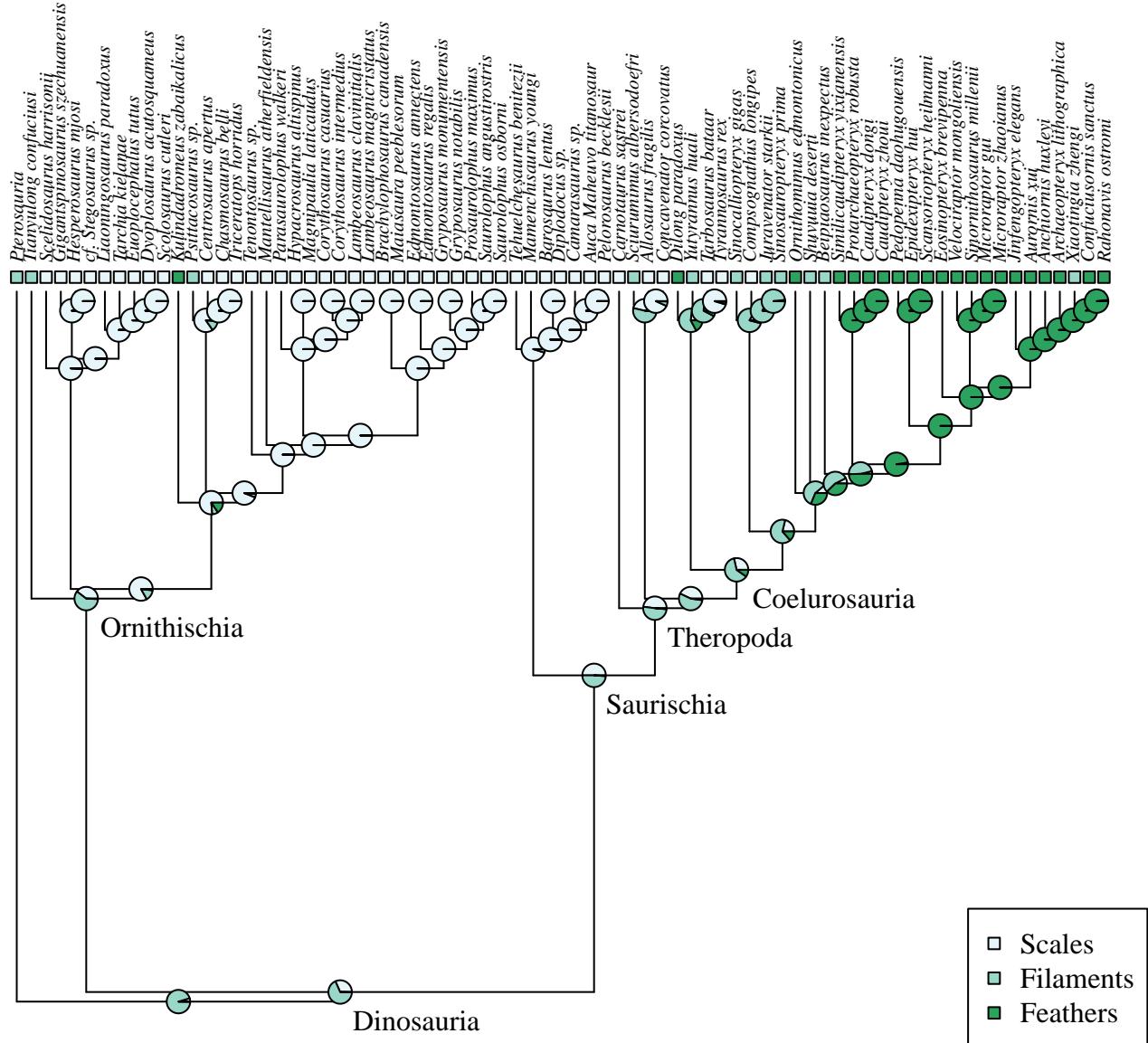


Figure S10. Ancestral states reconstructions using maximum likelihood along a time-scaled tree using the 'equal' time-scaling method. Integument treated as an unordered multistate character and the outgroup (Pterosauria) is coded as primitively filamented.

Multistate : Filaments : ordered : Equal

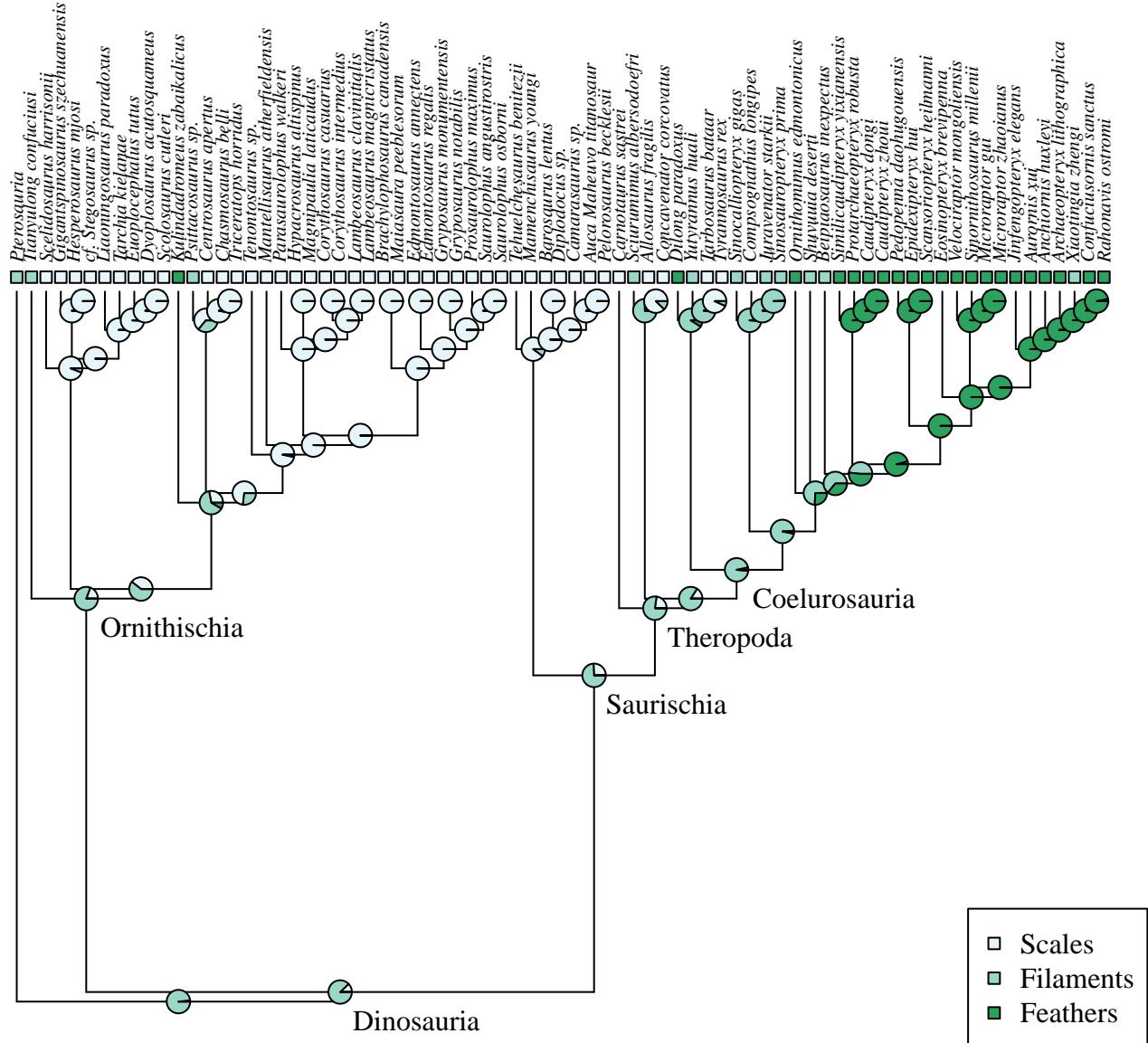


Figure S11. Ancestral states reconstructions using maximum likelihood along a time-scaled tree using the 'equal' time-scaling method. Integument treated as an ordered multistate character and the outgroup (Pterosauria) is coded as primitively filamented.

Binary : Filaments : unordered : Equal

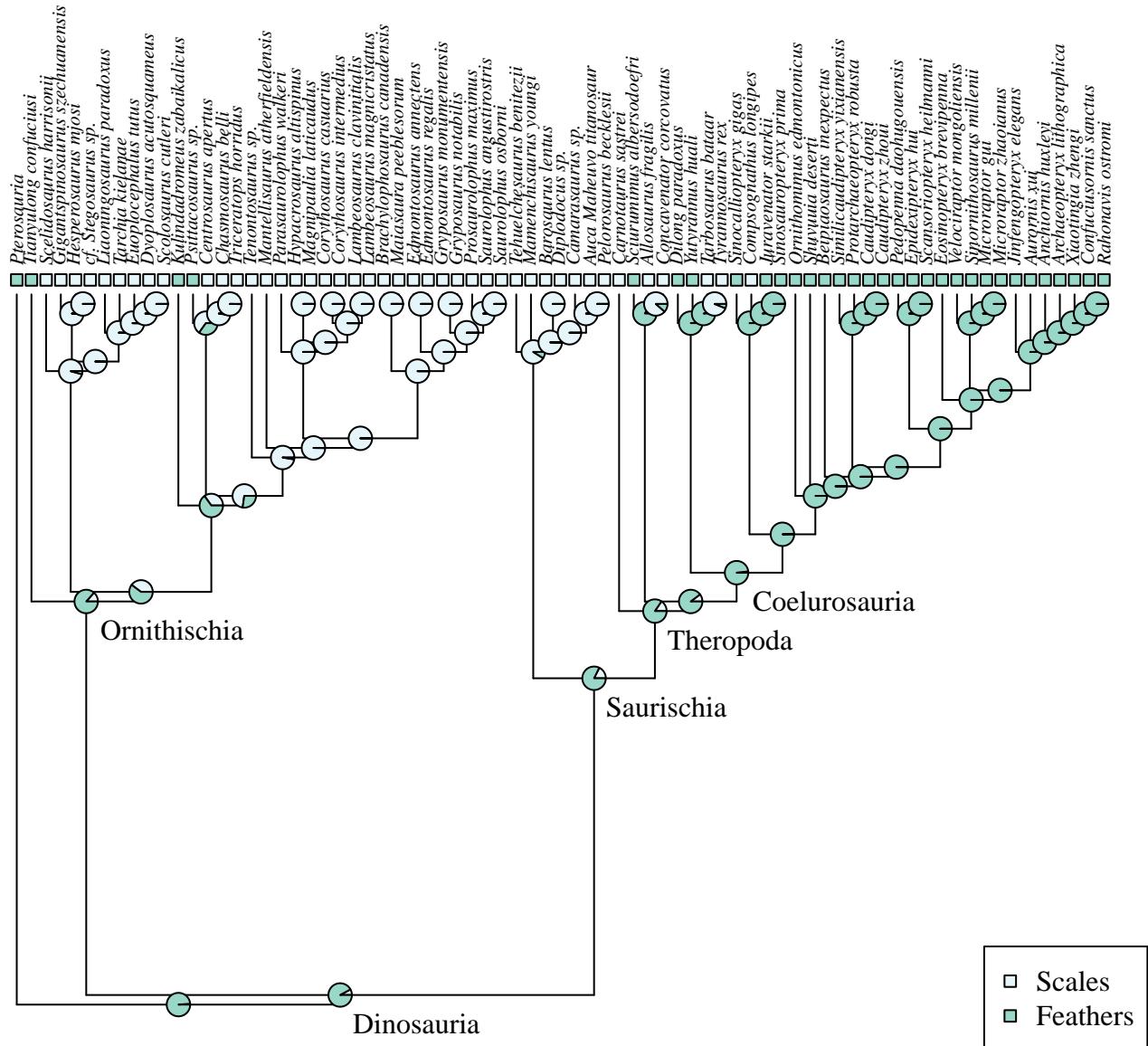


Figure S12. Ancestral states reconstructions using maximum likelihood along a time-scaled tree using the 'equal' time-scaling method. Integument treated as a binary character and the outgroup (Pterosaura) is coded as primitively feathered.

Multistate : Scales : unordered : Branches=1

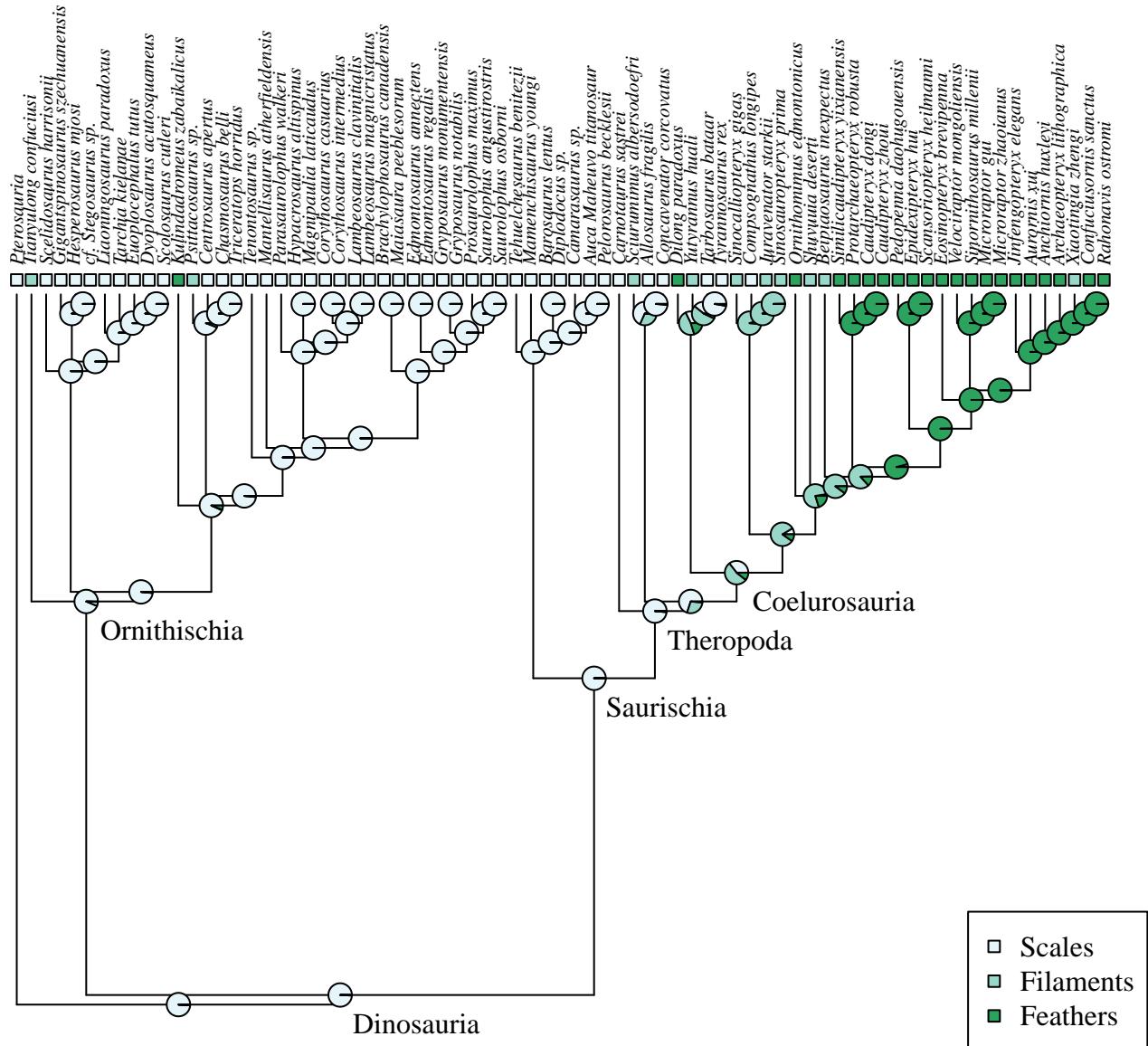


Figure S13. Ancestral states reconstructions using maximum likelihood along a tree in which branches are equally scaled to unity (all equal to one). Integument treated as an unordered multistate character and the outgroup (Pterosauria) is coded as primitively scaled.

Multistate : Scales : ordered : Branches=1

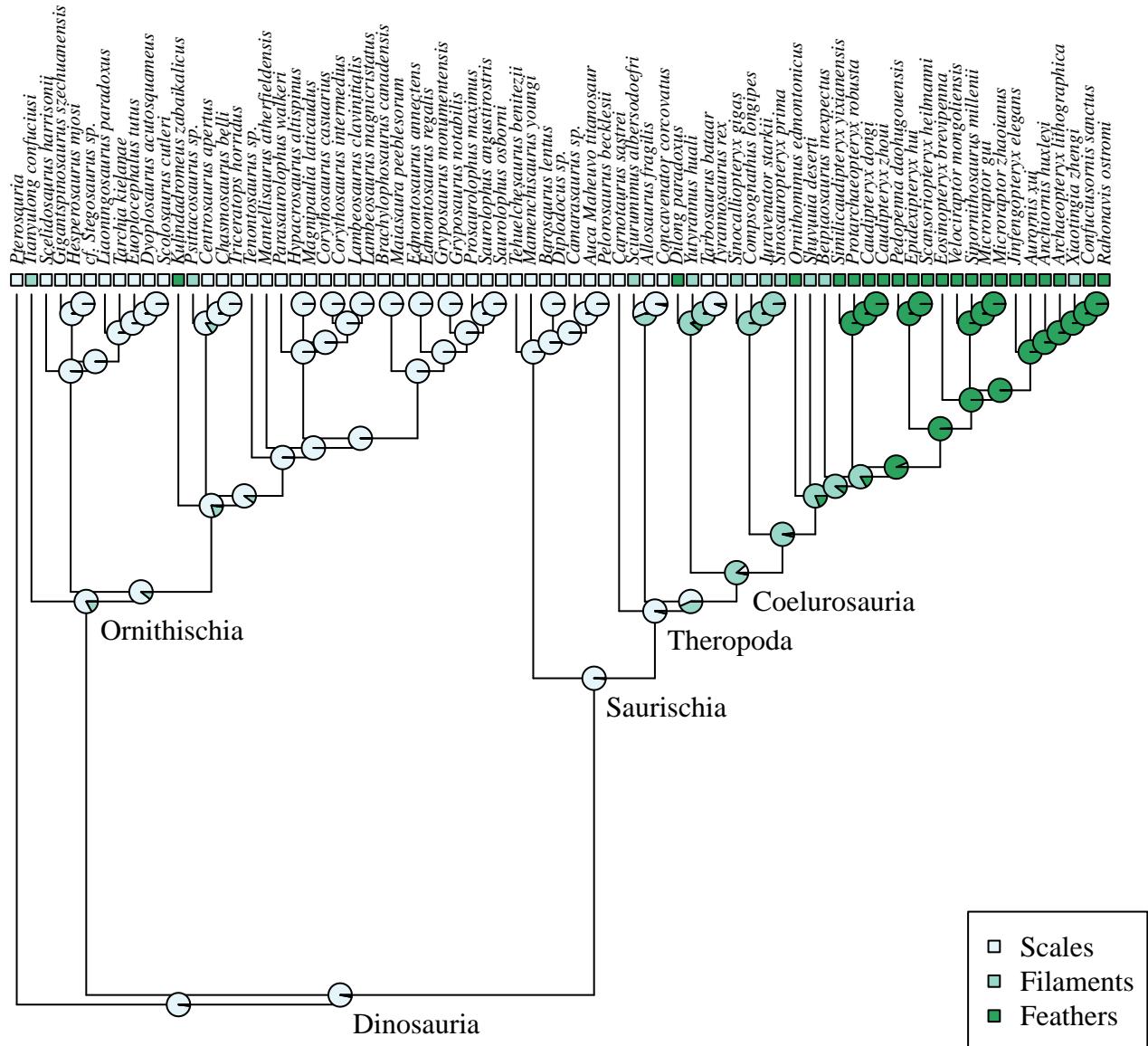


Figure S14. Ancestral states reconstructions using maximum likelihood along a tree in which branches are equally scaled to unity (all equal to one). Integument treated as an ordered multistate character and the outgroup (Pterosauria) is coded as primitively scaled.

Binary : Scales : unordered : Branches=1

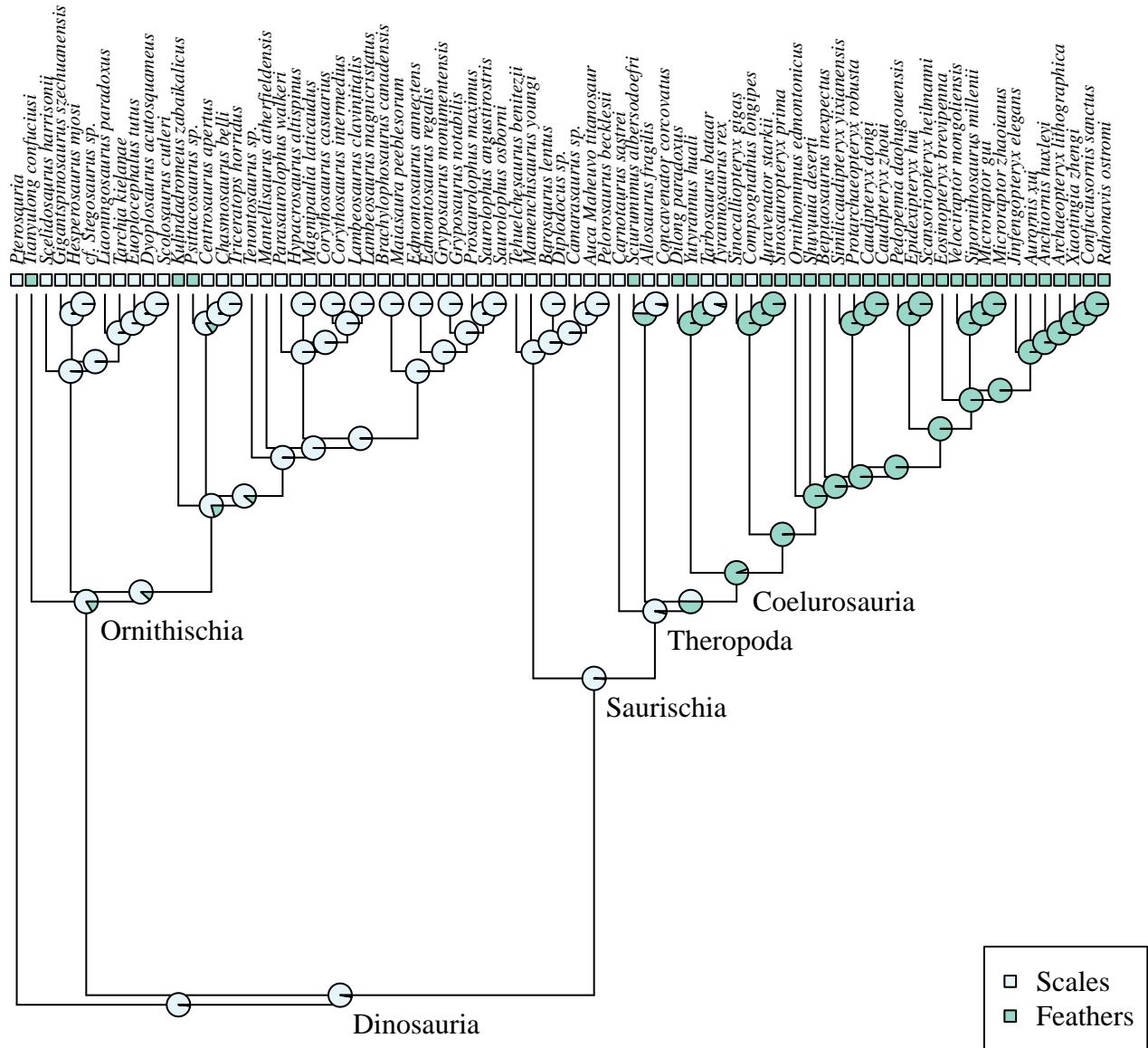


Figure S15. Ancestral states reconstructions using maximum likelihood along a tree in which branches are equally scaled to unity (all equal to one). Integument treated as a binary character and the outgroup (Pterosauria) is coded as primitively scaled.

Multistate : Filaments : unordered : Branches=1

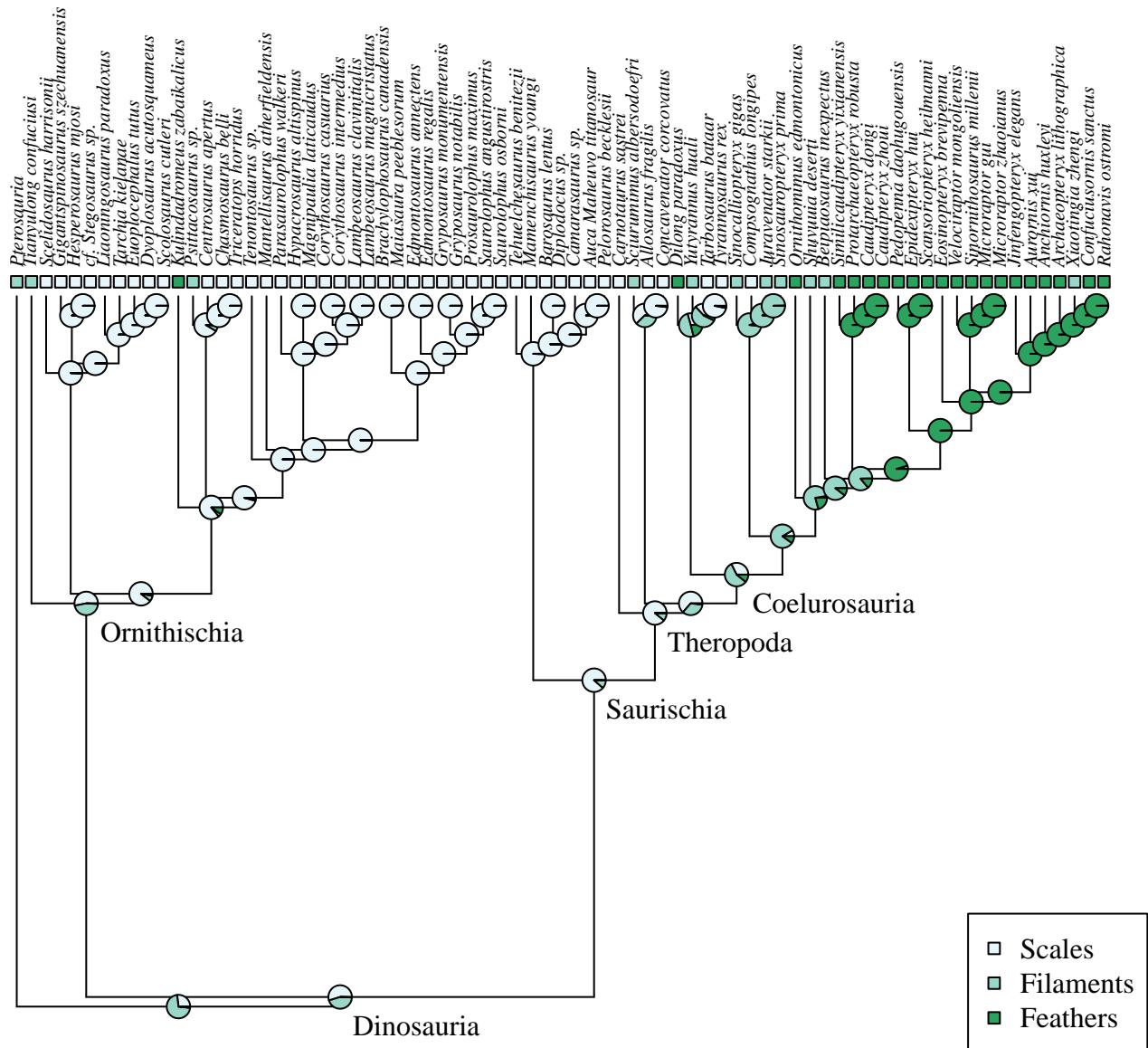


Figure S16. Ancestral states reconstructions using maximum likelihood along a tree in which branches are equally scaled to unity (all equal to one). Integument treated as an unordered multistate character and the outgroup (Pterosauria) is coded as primitively filamented.

Multistate : Filaments : ordered : Branches=1

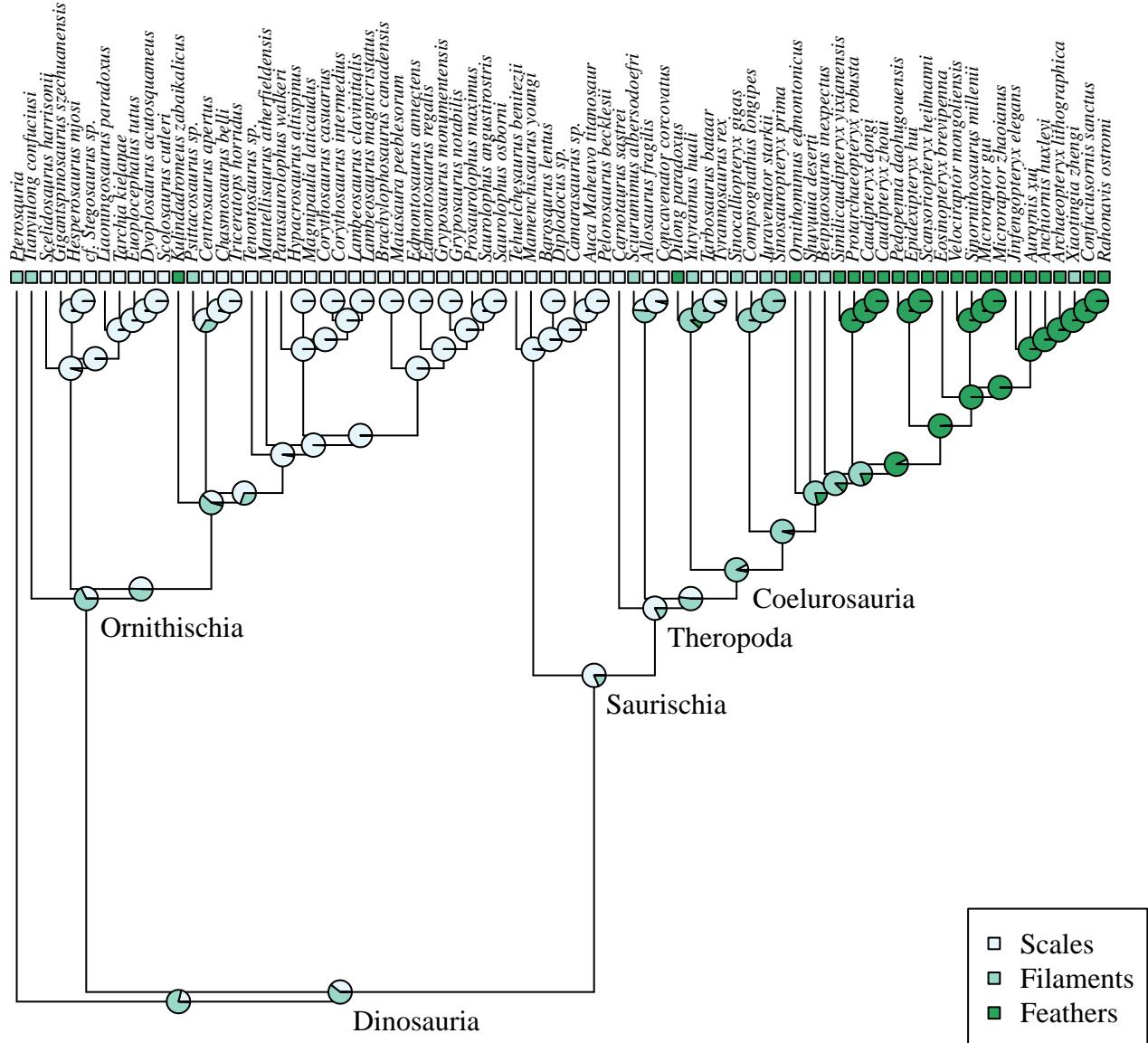


Figure S17. Ancestral states reconstructions using maximum likelihood along a tree in which branches are equally scaled to unity (all equal to one). Integument treated as an ordered multistate character and the outgroup (Pterosauria) is coded as primitively filamented.

Binary : Filaments : unordered : Branches=1

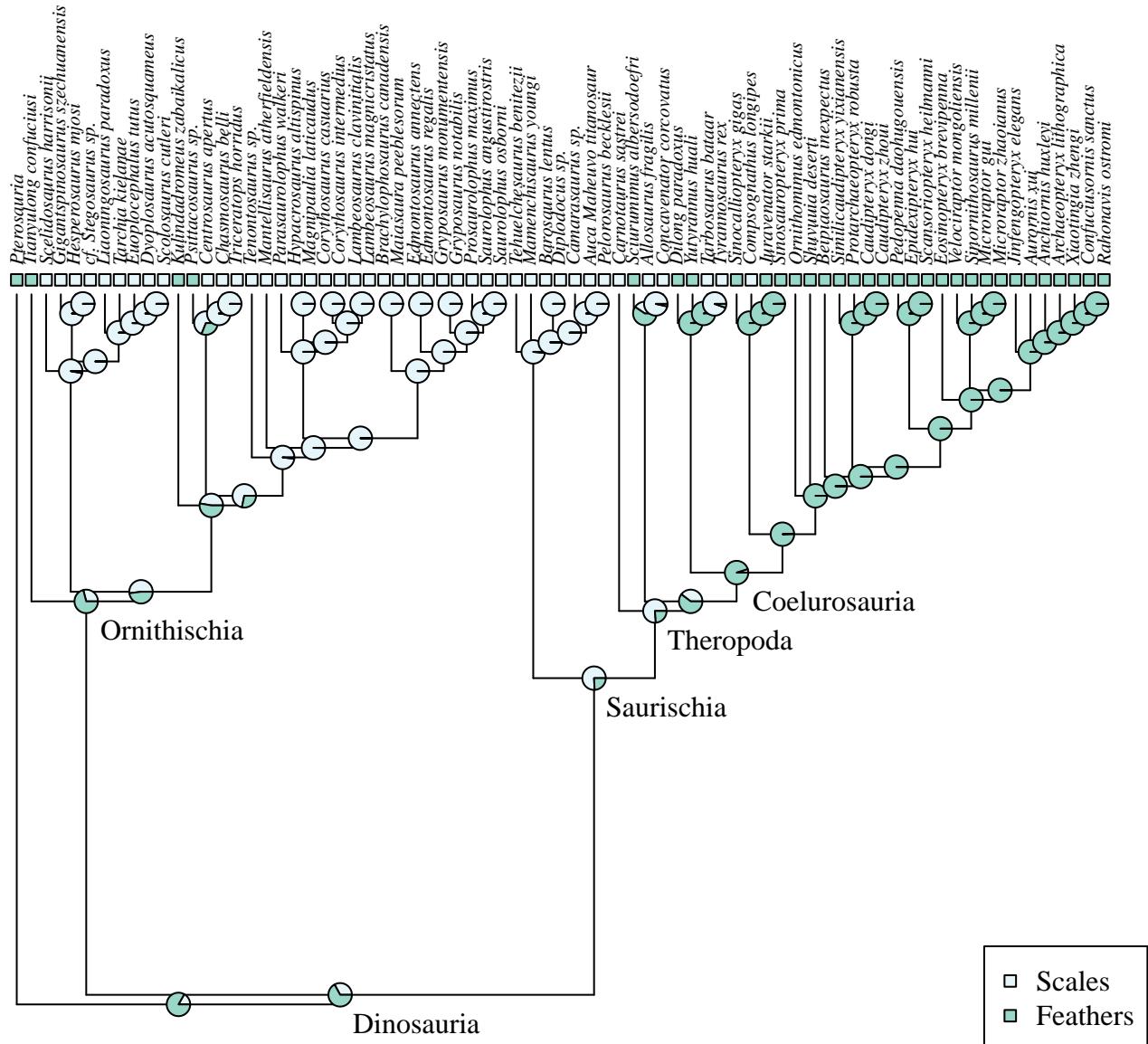


Figure S18. Ancestral states reconstructions using maximum likelihood along a tree in which branches are equally scaled to unity (all equal to one). Integument treated as a binary character and the outgroup (Pterosauria) is coded as primitively feathered.

TABLE S4. Results from maximum parsimony, DELTRAN and ACCTRAN optimisations of integumentary structures on to the combined dinosaur phylogeny, with different scoring and outgroup assumptions. The optimised conditions of the integument at key nodes are provided. Dinosauria, Ornithischia and Saurischia are generally recovered as primitively scaled regardless of the analytical protocol used. **Abbreviations:** **B**, presence/absence of filaments/feathers treated as a binary character; **F**, pterosaurs primitively covered in filaments; **M**, presence/absence of filaments/feathers treated as a multistate character; **O**, ordered character; **S**, pterosaurs primitively scaly; **U**, unordered character.

Optimisation	Dinosauria	Ornithischia	Saurischia	Theropoda	Coelurosauria
S B U Max	Scaled	Scaled	Scaled	Scaled	Filaments
S B U DEL	Scaled	Scaled	Scaled	Scaled	Filaments
S B U ACC	Scaled	Scaled	Scaled	Scaled	Filaments
F B U Max	Ambiguous	Ambiguous	Ambiguous	Ambiguous	Filaments
F B U DEL	Ambiguous	Ambiguous	Ambiguous	Ambiguous	Filaments
F B U ACC	Scaled	Scaled	Scaled	Scaled	Filaments
S M U Max	Scaled	Scaled	Scaled	Scaled	Ambiguous
S M U DEL	Scaled	Scaled	Scaled	Scaled	Scaled
S M U ACC	Scaled	Scaled	Scaled	Scaled	Filaments
S M O Max	Scaled	Scaled	Scaled	Scaled	Filaments
S M O DEL	Scaled	Scaled	Scaled	Scaled	Filaments
S M O ACC	Scaled	Scaled	Scaled	Scaled	Filaments
F M U Max	Ambiguous	Ambiguous	Ambiguous	Ambiguous	Ambiguous
F M U DEL	Ambiguous	Ambiguous	Ambiguous	Ambiguous	Ambiguous
F M U ACC	Scaled	Scaled	Scaled	Scaled	Filaments
F M O Max	Ambiguous	Ambiguous	Ambiguous	Ambiguous	Filaments
F M O DEL	Ambiguous	Ambiguous	Ambiguous	Ambiguous	Filaments
F M O ACC	Scaled	Scaled	Scaled	Scaled	Filaments

6. ANOVA OF MAXIMUM-LIKELIHOOD RESULTS

TABLE S5. Analyses of variation (ANOVA) of the effects of various parameters of overall likelihood values. ‘Pterosaurs’ refers to the assumed condition of the integument (scaly vs filament-covered) in Pterosauria; ‘model’ represents character treatment (ordered vs. unordered); and ‘tree’ refers to the branch scaling method (mbl vs. equal). See main text. The outgroup condition has the strongest effect on the nodal values, whereas the treatments of branch length and character scoring have weaker influences.

	Effect	df	Sum of Squares	Mean Square	F-statistic	P-value
Response: Scales						
Multistate	Pterosaurs	1	1.3859	1.3859	20.9233	<0.0001
	Model	1	0.3925	0.3925	5.9259	0.0182
	Tree	2	0.2075	0.1037	1.5662	0.218
Response: Filaments						
	Pterosaurs	1	1.3377	1.3377	24.5238	<0.0001
	Model	1	0.6228	0.6228	11.4177	0.0013
	Tree	2	0.3444	0.1722	3.1564	0.0503
Response: Feathers						
Binary	Pterosaurs	1	0.0004	0.0004	0.1252	0.7248
	Model	1	0.0265	0.0265	7.492	0.0083
	Tree	2	0.0527	0.0263	7.4472	0.0014
	Pterosaurs	1	1.3029	1.3029	13.9637	0.0009
	Tree	2	0.13926	0.0696	0.7463	0.484

7. SUPPLEMENTARY REFERENCES

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